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Resilience of experimentally-seeded dietary traditions in wild vervets: evidence from group fissions

Short title:

Resilience of traditions in wild vervets

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Abstract

Controlled laboratory experiments have delivered extensive and compelling evidence for the diffusion and maintenance of socially learned behavior in primates and other animals. Such evidence is rarer in the wild, but we show that a behavior seeded in a majority of individuals within vervet monkey (*Chlorocebus pygerythus)* groups may be sustained across several years. Here we report results of two natural fission events in such groups that offer novel evidence of the resilience of socially-transmitted group norms of behavior. Before fission, high ranked females exhibited an almost exclusive adherence to a group preference among two food options, originally introduced through a distasteful additive in one option, but no longer present in repeated later tests. Because of rank-dependent competition, low-ranked females ate more of the formerly distasteful food and so discovered it was now as palatable as the alternative. Despite this experience, low ranked females who formed the splinter groups then expressed a 100% bias for the preferred option of their original parent group, revealing these preferences to be resilient. We interpret this effect as conformity to either the preferences of high rankers or of a majority in the parent group, or both. However, given fissioned individuals' familiarity with their habitat and experimental options, we question the adequacy of the informational function usually ascribed to conformity and discuss alternatives under a concept of 'social conformity'.

Keywords:

Social learning, group fission, tradition, field experiment, conformity

Introduction

A wealth of experimental studies has now demonstrated the social learning of foraging habits and other behavior patterns in primates and in a wide variety of other species [Aisner &

Terkel, 1992; Galef, 1996; Galef & Whiten, 2017; Leadbeater & Chittka, 2009; Whiten, 2012; van de Waal, Claidière, & Whiten, 2013a; Zentall, 2012]. Such evidence is often strongest in laboratory or other captive contexts where experimental controls are most tractable to arrange, most importantly the provision of opportunities to learn from a model performing a novel action, contrasted with a no-model control condition, and/or to learn from either of two models displaying different behaviors. However, in the service of better understanding the implications of such social learning in the natural lives of animals, a small but growing number of experiments following these and other designs have now been engineered in the more challenging circumstances of the wild, providing evidence of social learning in a range of primates [Gunhold, Massen, Schiel, Souto, & Bugnyar, 2014a; Gunhold, Whiten, & Bugnyar, 2014b; Kendal et al., 2010; Schnoell & Fichtel, 2012; Schnoell, Dittmann, & Fichtel, 2014; van de Waal, Renevey, Favre, & Bshary, 2010; van de Waal & Bshary, 2011; van de Waal, Borgeaud & Whiten, 2013b] and other mammalian and avian species [Aplin et al., 2015; Slagsvold & Wiebe, 2011; Thornton & Clutton-Brock, 2011]. Additionally, new statistical techniques like social network diffusion analyses have offered complementary and compelling evidence for social learning in wild birds [Aplin et al., 2015], primates [Hobaiter Poisot, Zuberbühler, Hoppitt, & Gruber, 2014] and cetaceans [Allen, Weinrich, Hoppitt, & Rendell, 2013].

Social learning of diet and foraging behavior revealed in these studies creates the potential for diffusion of innovations that may spread to become traditions (group typical behavior shared by group members that relies on social learning), ranging from the short term to longer-term cases that may survive across generations [Mercader et al., 2007]. The evidence for animal traditions is also growing, yet remains more limited than for social learning *per se*, in part because the research required is inherently more demanding than the

basic 'A learns from B' paradigm that can be sufficient to identify social learning. Experimentally identifying the diffusion of socially learned behaviors necessarily involves tracking the spread across multiple individuals. Diffusion experiments of this sort have begun to proliferate, again particularly in the most readily controlled laboratory and other captive conditions [reviews: Mesoudi & Whiten, 2008; Whiten, Caldwell, & Mesoudi, 2016]. In one approach, called transmission or diffusion chains, a novel behavior is seeded in a founder model, who is then observed by a second individual who in turn becomes a model for the next, a process repeated to track transmission over multiple potential 'cultural generations'. A small set of such studies has identified transmission over as many as 6-8 such 'generations' in birds [Curio, Ernst, & Vieth, 1978], rodents [Laland & Plotkin, 1990] and primates [Dindo, Thierry, & Whiten, 2008; Horner, Whiten, Flynn E, & de Waal, 2006].

The control necessary to engineer such a linear series has, to our knowledge, unsurprisingly defied implementation in the wild. Instead an alternative approach called 'open diffusion' has been more feasible in the wild as well as in captivity [Whiten et al., 2016]. In this approach, founder models are trained to perform alternative behavioral solutions to naturalistic foraging problems and allowed to perform these within their group, with it being 'open' who watches and potentially learns from what is modelled, and the subsequent behavior of observers is subsequently monitored through further experimental presentations. Although only a few such studies have been completed in the wild, they have delivered positive evidence of diffusion, in birds [Aplin, Sheldon, & Morand-Ferron, 2013; Aplin et al., 2015], meerkats [Thornton & Malapert, 2009a] and monkeys [van de Waal, Claidière, & Whiten, 2015]. However the evidence for longevity in the alternatives that start to diffuse, and hence form incipient traditions, is more mixed. In many such studies the seeded options tend initially to be copied, but individuals' discovery of the alternative option may then erode the

behavioral differences over time, such that stable alternative traditions are not necessarily sustained [Kendal et al., 2010; Schnoell & Fichtel, 2012; Thornton & Malapert, 2009b; van de Waal et al., 2015].

Given evidence for a basic form of 'conformity' in animal social learning, whereby individuals show an adaptive bias to 'copy the majority' [Claidière & Whiten, 2012; Haun, van Leeuwen, & Edelson, 2013], the spread and stabilization of seeded innovations in such experiments may be an example of social learning that is inherently limited by a reluctance to copy relatively rare behaviors, or behaviors shown only by only one or a few individuals. Given this consideration, van de Waal and colleagues [2013b] explored an alternative approach in which whole groups of vervet monkeys were seeded with alternative behavioral options and the responses of naïve individuals experiencing these apparent existing traditions were recorded. In this case the alternative behaviors involved preferring to eat maize of one color, and avoiding another color that signaled an aversive and bitter taste. Once the two provisions were later made equally palatable, the social learning responses of two categories of naïve others (new infants and migrating mature males) were recorded. In both infants and immigrant males, potent social learning was found, consistent with a 'copy the majority' bias noted above, especially in the case of the migrant males [Whiten & van de Waal, 2016]. This effect therefore offers an important context in which to further investigate the resilience of experimentally seeded traditions once they are common in the group. In this paper we report the results of repeated testing over a period of 22 months.

Events in which small groups of low-ranking females split off from one large group, which occurred on two different occasions, are of particular interest here because of the behavior they later revealed. Female vervet monkeys have a strict linear dominance arranged according to matrilines within each group [Cheney & Seyfarth, 1990]. We observed

permanent group fissioning from our largest group (over 50 individuals before the first fission) Baie Dankie (BD). The 'In Betweeners' (IB) was the first splinter group from BD during our three years of studying four groups of vervet monkeys, and Intaka (IN) group was the second to split from BD, after four years of studying these four groups. Since 2014 the field site has experienced a drought, so fissions may occur when food resources are scarce and the group has become too large to share these well. In the pioneer and only long term study of a vervet monkey population in the Amboseli Park in Kenya, group fusions were documented [Jaffe & Isbell, 2010], but not group fission [Robert M. Seyfarth. pers. comm.]. To our knowledge we report here the first fissions in vervet monkeys. However dispersal by the fissioning of an established group is well-documented in many other old world monkeys [e.g., blue monkeys: Cords & Rowell, 1986; Cords, 2012; redtail monkeys: Struhsaker & Leland, 1988; Japanese macaques: Koyama, 1970; Sugiyama, 1960; rhesus macaques: Chepko-Sade & Sade, 1979; long-tailed macaques: van Schaik & van Noordwijk, 1988; and savannah baboons: Nash, 1976].

As we show below, because of their low rank in the parent group, the individuals in our splinter groups had earlier gained significant personal evidence that both food colors denoted palatability and edibility. The fact that low rankers are more opportunistic and flexible in their feeding behavior than high rankers was nicely demonstrated in cooperatively breeding birds [Keynan, Ridley, & Lotem, 2015]. The individuals that we studied in the fissioned groups therefore provided a particularly pointed test of the effects of social learning on long-term behavioral biases: would females in these splinter groups, who already deviated most from the predominant pattern in their group, be the most likely to show further

degradation of the seeded bias in color preference? Or would they now more freely express this bias, such that it would be traditionally maintained in the new groups?

Methods

Study populations and field site

The study was conducted between August 2011 and September 2014 as part of the Inkawu Vervet Project (IVP) in a 12,000-hectares private game reserve, "Mawana", in KwaZulu Natal, South Africa (S 28° 00.327; E 031° 12.348).

Subjects were vervet monkeys, *Chlorocebus pygerythus*, in six habituated groups; four main groups and two splinter groups that divided from these. Such division is often referred to in the literature as group fission, but here we prefer the term 'splinter' to denote that two very small groups were created, leaving behind one still-large group. Aside from these small splinter groups, monkeys lived in stable groups which varied from 24 to 56 individuals. In our population, all groups are distributed along a river, and each group's home range overlaps with those of multiple neighboring groups. Average home range size was ca. 160 hectares. Groups typically contained an alpha male, subordinate males and several matrilines (females and their offspring). Male vervets migrate to other groups when they are sexually mature (usually around 4 years of age), while females usually remain in their natal group throughout their lives. Vervet monkeys have a linear dominance hierarchy manifested in relation to matrilines within the group; high-ranking females and their close relatives (mothers, sisters, and daughters) are the most sought-after grooming partners [Isbell, Pruetz, Lewis, & Young, 1999]. High-ranking females enjoy priority access to food during foraging bouts and have access to higher quality food, which greatly increases their yearly food intake compared to lower- and mid-ranking females [Whitten, 1983]. The dominance hierarchy at IVP is assessed by the creation of matrices based on dyadic aggressive interactions (i.e., winner- loser)

occurring either in a natural context or around various food experiments. Using the "I&SI" method of de Vries [1998], we found that the female hierarchy was stable during the study period whereas the male one was highly variable [Borgeaud, Sosa, Sueur, Bshary, & van de Waal, 2016].

The present study focused on two recent group splits in the largest group (including a maximum of 56 individuals during this study) of our study population. First, in 2012, six individuals left 'Baie Dankie' (BD) group and formed the 'In-Betweeners' (IB) group; a year later, in 2013, three other individuals left BD group and formed the 'Intaka' (IN) group (Fig. 1 and Table 1; more details in results section). We considered each splinter group as independent from their origin group, once they had been sleeping in different sleeping sites than their origin group for over a month, and encounters with their origin groups were agonistic, similar to those with other neighboring groups. Therefore the splinter groups had no opportunities for observational learning from their original group after they fissioned. All individuals were identified, mainly by facial cues. A recognition file with portrait photographs as well as specific individual features (scars, color, etc) was maintained for each group.

Experimental procedure

The initial training phase consisted of three sessions, conducted at monthly intervals, where two adjacent boxes of maize, one dyed blue and one pink, were offered to the monkeys. Both boxes of maize where soaked overnight in plain water with food coloring in it, and in one box of maize mountain aloe (*Aloe marlothii*) leaves were added giving it a very bitter taste and smell, unpalatable for the monkeys. For two groups the aloe-treated maize was dyed blue ('Lemon Tree' (LT) and 'Noha' (NH) groups), for two others, pink ('Ankhase' (AK) and BD groups). These training sessions provided about 2 kg of maize for the groups, that ranged from 30 to 43 individuals during the three training sessions, so less than 70g per individual on

average. Boxes were refilled to ensure that monkeys always had a choice and that as many group members as possible participated. Training and test sessions were unrestricted in time, lasting as long as individuals were feeding so as to have as many group members as possible participating (for the initial six tests in the four large groups pre-fission: minimum length 97min, maximum length=4h32min; the splinter group trials: IB=31min, IN=43min).The side of the pink and blue maize was alternated across the three training sessions and the six test trials, as viewed from the camera and researchers' perspective.

The subsequent experimental phase for the four trained groups consisted of six test trials spaced at intervals of 1, 1, 2, and 4 weeks, then approximatively 6 months, with two boxes containing the same two colors of soaked maize, but with one major exception: no maize was aloe-treated. Thus, all maize was now palatable and edible. Observational data were collected only 48h after each provisioning [van de Waal et al., 2013b].

After each of the two group fissions noted above, we tested the new splinter group on its own as soon as possible, which took several months to achieve. The new groups did not include any individual with a VHF collar so were not easy to locate, in addition to which they were highly mobile in establishing their new home range and avoiding large neighboring groups. They were also relatively shy so testing was delayed until winter when they were most motivated to participate in test sessions. As a result tests occurred seven months after fission for IB group, and over a year later for IN group.

As both group splits occurred in the same group, BD, which had earlier been trained to eat blue maize, we designed an additional test to investigate low-ranking females in a pink-trained group. We conducted these experiments on the seven lowest-ranked females of NH group, a group well habituated to human researchers. We targeted each of these females while she was alone (or just with her own offspring) and offered her a small box with two compartments filled with the two colors of maize. We conducted these experiments at the end

of the South African winter in September 2014, when the natural food of the vervet monkeys is scarce, and the monkeys spread out after they leave the sleeping site. We presented the food for a maximum of 10 minutes or until other group members approached.

Data collection and analyses

All experiments were recorded using a video camera on a tripod. The image included the two boxes and approximately 1 meter on each side. In addition, on each minute we recorded who was eating at the boxes. A minimum of two observers conducted and recorded the experiments in the four trained groups. As the splinter groups were relatively shy to human observers we initially conducted the experiments with the camera on a tripod without any researchers nearby, and later with only one researcher in IB group, then initially with only one researcher, then two, in the IN group.

We applied a focal sampling method during the field experiments, and where necessary in supplementary video analysis, to record each individual processing (eating or spitting out) up to seven pieces of maize of each color per session. Coding was unambiguous as it was always conducted when feeding individuals were facing the observers and the color of the maize was easily visible.

All statistical analyses were performed using IBM SPSS 22. Because the splinter groups provided only small sample sizes, two-tailed non-parametric analyses are applied throughout. Non-parametric tests are robust for our multiple measures on the same individuals [Chen & Popovich, 2002].

Ethics

The experimentation reported in this paper followed the American Society of Primatologists' Principles for the Ethical Treatment of Primates. The study was registered

with Ezemvelo KZN Wildlife in South Africa and the experiment including use of aloe to create a distasteful sample of food was approved by the Ethics Committee of the School of Psychology and Neuroscience, University of St Andrews.

Results

Rank predicts adherence to modal group preferences

Following the original 2011 aloe training described above, we offered the choice of the two colors of maize, now untreated and thus palatable, in repeat tests run up to 2014. We found that a strong correlation had emerged between the percentage of time that a female spent eating the locally preferred color and her rank in the group's dominance hierarchy, with the highest-rankers exclusively eating the original, always palatable color and ignoring the originally aloe-tainted, but now equally palatable, alternative (Spearman correlation, N=26 (the females who participated in all 6 trials), Rho= -0.730, P<0.001; Fig. 1a, see supplementary Fig. 1 and video 2; Spearman correlation, N=36 (all females that participated at least in 1 trial), Rho=-0.447, P=0.006). Inspection of individual profiles (Fig. 1b) indicated that this effect was mainly caused by the lowest ranked females in each group (boxed in figure), who in the competitive context of the maize provisioning, took much more of the originally distasteful but now perfectly palatable color of maize (Fig. 1b).

Change in expressed preferences of fissioned groups females

The recent group fissions documented above revealed a prioritization of social over personal information. These fissions occurred after the behavioral patterns illustrated in Fig. 1 were established. Both small splinter groups (see Table 1 for individual details) came to occupy home ranges that overlapped that of the parent group, BD (Fig. 2).

Comparing the time spent eating blue versus pink maize before vs. after the group fissions we found a significant change in color choices. Although all IB females ate both colors in the original BD group (individual Oo is a male, see Table 1), they ate exclusively blue maize during the first test after having separated from the higher rankers of their original group, whose members displayed a strong preference for blue maize. The IN females similarly ate both colors while still in BD but ate only blue maize during the first test after the fission (Wilcoxon signed-rank test of change in percentage of blue taken, including (i) all individuals of both splinter groups: Wilcoxon signed-rank test, N=9, Z=-2.52, P<0.02, and (ii) with only the adult females of both splinter groups: Wilcoxon signed-rank test, N=6, Z=-2.20, P<0.05; Fig. 3a, b, see supplementary Fig. 3).

The strong bias of these females towards the majority preferences of the parent BD group occurred despite the fact that all had substantial direct, prior personal experience that both foods were equally palatable (and some had equal or even more experience with the locally non-preferred color), for they had fed on pink maize in repeated but separate episodes during an average of 9.2 one-minute samples (s.d ± 3.3) spread across the experimental trials, before the fission events (details in Table 2).

Control test excluding basic color preference

Further analyses explored and tested potential explanations for the bias. First is the possibility that vervet monkeys simply have a basic preference for blue over pink food items. Because no splits occurred in pink-trained groups, which would have provided cross-confirmation of the results from the blue trained group, BD, we tested the seven lowest-ranking females in the two pink-trained groups while they were not in association with higher-ranking competitors, offering the small boxes with compartments of pink and blue maize, as described above. We found an all-but-exclusive preference for pink in these solo tests (percentage time spent eating

this preferred color: N=7, median = 100 and mean = 99.7), much stronger than these same females had expressed in earlier group tests (Wilcoxon signed-rank test, N=7, Z=-2.20, P<0.05; Fig 4, see also supplementary Fig. 4 and video 5). This finding confirms there is no general bias towards a preference for blue maize. These results are also consistent with those observed after the group splits (i.e. that low-rankers prefer the majority choice, even if they do not, or cannot, select it in a group setting).

Confirmation of a socially learned effect

A second analysis served to examine the possibility that once females had split from higher-ranked group mates, the strong preference they expressed could simply be one all monkeys had learned individually from their original training experience of aloe-treated food, and could return to now that they had the opportunity to do so. This scenario is not supported because we found that only one of the six females forming the IB and IN groups had taken treated maize into her mouth during the original training events. Moreover, only one of the seven low-ranking females in the pink-trained group (NH) that were tested alone ate one piece of aloe-treated maize, a single time. More generally, of the 39 females from our four groups present during the original aloe training, only 20 directly sampled aloe-treated maize (meaning taken in hand or mouth a piece of maize), and a similar number, 19, never touched a piece of the aloe-treated maize. These 19 females that had never smelled or tasted the treated maize subsequently ate for a mean percentage of time intervals 86.6% of blue maize in the blue trained groups and 16.2% in the pink trained groups during 6 pre-fission tests, percentages not significantly different from the 77.6% and 13.6% respectively, for the 20 females that had learned by direct experience of treated maize (Mann-Whitney U test, N=39, U=181.5, P=0.811; Fig. 5a, b). These results indicate that for half of all the females in our experiments, the persistent preference they expressed was not based on their own past direct

experience, but instead on social learning, likely resulting from often strong observational cues that one alternative was very distasteful, such as monkeys throwing pink maize away or spitting it out. Encounters of the splinter groups with neighboring groups, even with their original group, were always aggressive. Accordingly they could never observe other groups feeding on the colored maize, so there were no further opportunities for social learning. The color preference must have been derived from pre-fission learning.

Results from a group tested with no aloe training underline the resilience that vervets may display once a dietary preference is expressed by a majority. When this group, Kubu, was offered the two colors of maize, the alpha male started eating pink, but the alpha female started eating blue. The alpha male ate first, then the alpha female came and ate when the alpha male was still eating. She was joined by two others that also ate blue. Then both alphas left and the four other monkeys started eating blue. The alpha male ate only pink during the first trial, but then he switched and ate only blue at the second trial, and maintained a preference for blue in the following trials up to the seventh trial. Over the course of seven tests this group, that never tasted any bitter-tasting aloe maize, displayed as strong and resilient a preference for one color as the aloe trained groups (mean percentage of time eating preferred color over trial 1 to 7, in the four trained groups = 70.4% ; in Kubu group = 69.2%).

Copying high-rankers or a majority?

A third and final issue is whether the social learning effect is based on the monkeys' observation of just one or a few individuals, such as high ranked animals, or the alternative of copying a majority (a criterion for 'conformity' preferred by many [Battesi, Moreno, Joly, & Mery, 2012; Henrich & Boyd, 1998; van Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; Pike & Laland, 2010] though not all authors [van de Waal et al., 2013b]. As Fig. 1 shows, a bias to copy the highest-ranked animals could produce a similar effect to copying the

majority and we cannot definitively distinguish these. However, we found that the array of monkeys that others could view was consistently and repeatedly displaying a clear majority at one of the two colors (Fig. 6a), and that the cumulative majority of individuals eating blue that monkeys could easily have observed before the group splits rose steadily during the experiments (Fig. 6b). Thus information that could inform conformity was clearly readily available. In the discussion we explain why perception of these majority displays and conformity to them may offer the most parsimonious explanation for the behavior of the splinter group females.

Discussion

The six females in the two splinter groups, tested several months after the split, showed a 100% bias for the dietary preference shown by a majority of their parent group, and we have presented data rejecting the possibility that this reflects an inherent color preference or an earlier, individually learned preference. Accordingly these results lead us to conclude that the strong preferences are socially learned traits. The existence of such dispositions could potentially thus support traditions resilient to major perturbations in the social fabric of groups such as the fissions we documented. Given that only one of the fissioning females had ever directly mouthed aloe-treated maize and that all these individuals had direct experience that both colors were palatable and had no side effects, their 100% commitment to their origin group color preference is striking.

An explanation for the strength of this effect might lie in the fact that ours is so far the only study to seed local habits in a *majority* of each group. The handful of other field experiments that have seeded alternative behaviors in the wild have typically done so in only single individuals initially, and these studies have tended to demonstrate initial social

learning, soon followed by corruption and erosion of group behaviors, rather than the resilience so marked in our own study where we instead simulated existing customary traditions [Kendal et al., 2010; Schnoell & Fichtel, 2012; Thornton & Malapert, 2009b; van de Waal et al., 2015]. Another potential explanation is that our experiment is the only one testing a preference for a food type rather than including an object or 'artificial fruit' manipulation like those cited above. Using social information to make adaptive food choices may be a more habitual process than learning manipulative techniques.

What decision rules of these females explain such effects? Two principal options appear to fit our findings. One is that the fissioning females were motivated to try to act like the highest ranked females they had witnessed in their parent group, who expressed the strongest preference for the maize color favored by the group (Fig. 1). Such preferential copying of high ranked individuals has been shown in captive primates (chimpanzees) and suggested to be adaptive insofar as high ranking individuals are often the most successful foragers and therefore best to copy [Kendal et al., 2015; Horner, Proctor, Bonnie, Whiten, & de Waal., 2010]. In the wild, Hobaiter and colleagues [2014] found evidence of a dominant individual (the alpha male) seeding a behavior (using moss for water sponging) in a chimpanzee community, and this has now spread further [Lamon, Neumann, Gruber, & Zuberbühler, 2017]. However to our knowledge, such an effect has not been shown experimentally in the wild, to date. If this motivation was responsible for the effect, it survived the severing of the association with these high ranking females by at least 4 months.

A second alternative is adopting the preference shown by a majority of the parent group, a form of conformity [Haun et al., 2013], although in this case based on long term memory of majority behavior in the parent group, BD. Such effects have been documented in

other animals including birds [Aplin et al., 2015], and male migrants in our own study population [van de Waal et al., 2013b; Whiten & van de Waal, 2016]. In the results section we documented that there was a visible majority available for the individuals to copy the color choice before they fissionned (Fig. 6). However as it was logistically not feasible in the field to gather data on the attention of bystanders around the colored food, we cannot discriminate if this was key in the current study. We do think it feasible to experimentally test for a bias to copy high rank models in future, although this is far from straightforward to engineer. We suggest that of the two potential rules, this would thus appear to be the more cognitively economic to implement, compared to one that requires integration of (i) knowledge of the ranks of group mates; (ii) a running tally of the preferences of each and (iii) a comparison of these tallies. We know that resident vervet monkeys do in fact acquire a good working knowledge of rank relationships in their group [Borgeaud. van de Waal, & Bshary, 2013; Seyfarth & Cheney, 2015], so this hypothesis deserves to be investigated and experiments to do so are ongoing in our research program. In the meantime, copying the majority appears the most parsimonious of the two processes likely to underlie the resilience our data demonstrate. Of course the two potential rules are not mutually exclusive: both may be in operation here and may mutually reinforce each other to maintain group traditions long after the original conditions that created them have passed. Either way, the mechanisms involved produced a remarkable resilience in the preferences established through social learning, even after major changes in social context and in the face of personal information that could have led to an erosion of these preferences.

A major issue therefore concerns what functions such resilient group-level preferences may serve. Here we suggest that a distinction between what social psychologists call informational versus normative conformity provides a helpful framework [Claidière &

Whiten, 2012; Deutsch & Gerard, 1955]. Informational conformity serves the function of providing good, truthful information about the world; in the present context this concerns which is the best of two food options to consume. Normative conformity, by contrast, serves purely social functions, such as strengthening bonds with others by simply being more like them, or adhering to societal or even prescribed norms. In our experiment, copying either high rankers or a majority of others might in principle serve an informational function, insofar as high rankers tend to eat the 'best' foods, and a majority of the group has likely converged on the optimal choice too. However, neither of these rationales fit well with the circumstances of the fissioning females, who already had good personal information on the palatability and safety of eating either of the food colors on offer. Moreover, unlike the male migrants for whom we earlier reported conformity to the new and different preferences of their adopted group [van de Waal et al., 2013b] and so perhaps had need of local adaptive information, the females had not moved far, partly occupying the same familiar area, and even sometimes feeding on the same provisioning sites as before.

Accordingly we suggest we should explore the hypothesis that the females' behavior could constitute what we here provisionally call 'social conformity'. By social conformity we mean that individuals act like others not to achieve an informational function, but instead to achieve a social function that derives from simply 'being like others' as suggested by the bonding and identification-based observational learning (BIOL) theory [de Waal, 2001], despite other options being open to them (in the present case, selecting only one of two food options they know are equally palatable). Such a disposition may need no underlying complex cognition, but merely the following of a motivational rule, that might have innate or learned origins or both. If the rule were to preferentially act as the majority do, such conformity could normally assist intra-group integration, important for a range of outcomes including

coordinated travelling and foraging, and mating opportunities. If the rule were to preferentially act as high-rankers do, such conformity could make performers appear of superior status (we are aware that referring to conformity here deviates from the common usage denoting copying a majority), but we apply it to highlight that the individual would be ignoring alternative actions open to it and copying 'just to be like others', another common way in which the term conformity is used.

'Social conformity' thus contrasts with informational conformity in a similar way as does social psychologists' 'normative conformity', but we use a different term because normative conformity is often taken to require a recognition that norms *should* be followed (i.e. that norms are prescriptive and deviations may be punished), although in fact some psychologists in any case divide norms into either prescriptive norms (what it is proper to do) or merely descriptive norms, which describe the statistical property of what a majority do (easily applied to non-human animals, as indeed we do here). In children recognition of the prescriptive, normative aspect of conformity emerges early in childhood, as in experiments where, for example, children object when a peer or even a puppet transgresses an arbitrary conventional norm [Keupp, Behne, & Rakoczy, 2013; Rakoczy, Warneken, & Tomasello, 2008].

We speculate that the more elementary possibility we have called social conformity may nevertheless turn out to be a significant phenomenon in nature, given the importance for group-living animals of meshing one's social dealings with others [Silk, Alberts, & Altmann, 2003; Silk, 2007; de Waal & Lutrell, 1986]. There is evidence that primates are more affiliatively disposed to those who match their own behavior [Nielsen, Collier-Baker, Davis, & Suddendorf, 2005; Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005; Paukner,

Suomi, Visalberghi, & Ferrari 2009]. Social conformity effects related to this could be important, for example, in explaining tendencies in birds [Catchpole & Slater, 2008; Lachlan, Janik, & Slater, 2004], whales [Garland et al., 2011] and primates [Watson et al., 2015] for vocal convergence among associating individuals. Whatever the underlying explanation for the behavior we recorded in our vervet splinter groups, the strength of their inclination to persist in the choice of the dietary option prevalent in their parent group despite their knowledge of perfectly viable alternatives demonstrates a marked resilience in a primate tradition documented in the wild.

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Figure legends:

Figure 1: a) Correlation between adult females' rank and the average number of minutes spent eating the initially palatable color during experiments 1 to 6, for all females who participated in all 6 trials. The black line represents the power trend line. Pink points represent females from the two groups trained to eat pink (NH: blue line around data points, LT: black line around data points), blue points represent females from blue trained groups (AK: black line around data points, BD: pink line around data points). b) Time spent by each female eating the initially palatable color for each group. Number in brackets next to name code shows female's rank. Boxes around results highlight the reduced time spent feeding on the preferred color by the lowest-ranking females of each group.

Figure 2: Map of the home ranges of two groups In Betweeners and Intaka that split from Baie Dankie group.

Figure 3: Average percentage of minutes spent eating the preferred color ('local preference') compared to the other color ('other') by individuals before (all recorded trials pre-fission where the individuals participated) and after split (1st trial) from the original BD group: a) for IB individuals; b) for IN individuals.

Figure 4: Average time (in minutes) spent eating the preferred color by low-ranking females of NH, in the group context and when tested alone.

Figure 5: Average % of observed minutes eating maize of each color in both pink- and blue-trained groups: a) females that tried aloe maize during the training phase (n=20); b) females that never picked up a single maize piece treated with aloe (n=19).

Figure 6: a) Mean number of BD monkeys eating the preferred color (blue) and the alternative color (pink) collected in 10-minute scans and expressed during the first two hours in experiments 1-6. b) Mean cumulative number of BD monkeys eating the preferred color (blue) and the alternative color (pink) across successive scan periods. Supplementary Fig. 6. Mean cumulative number of BD monkeys eating the preferred color (blue) and the alternative color (pink) across successive scan periods during the first two hours in Experiment 1.

Highlights

- First report of group fission in vervets reveals high tradition resilience
- Initial group was trained to prefer one of two foods but low-rankers sampled non-preferred option
- After fission these monkeys ate only the parent group's preferred option

Fig. 1

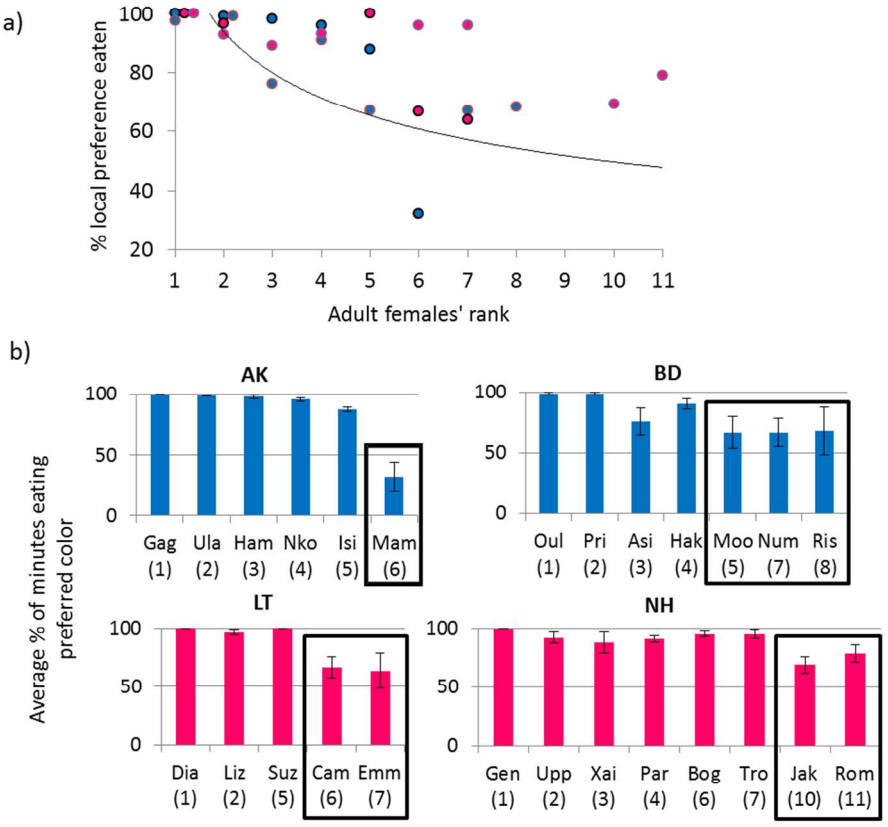

Figure 1: a) Correlation between adult females' rank and the average number of minutes spent eating the initially palatable color during experiments 1 to 6, for all females who participated in all 6 trials. Pink points represent females from the two groups trained to eat pink (NH: blue line around data points, LT: black line around data points), blue points represent females from blue trained groups (AK: black line around data points, BD: pink line around data points). b) Time spent by each female eating the initially palatable color for each group. Number in brackets next to name code shows female's rank. Boxes around results highlight the reduced time spent feeding on the preferred color by the lowest-ranking females of each group.

182x175mm (150 x 150 DPI)

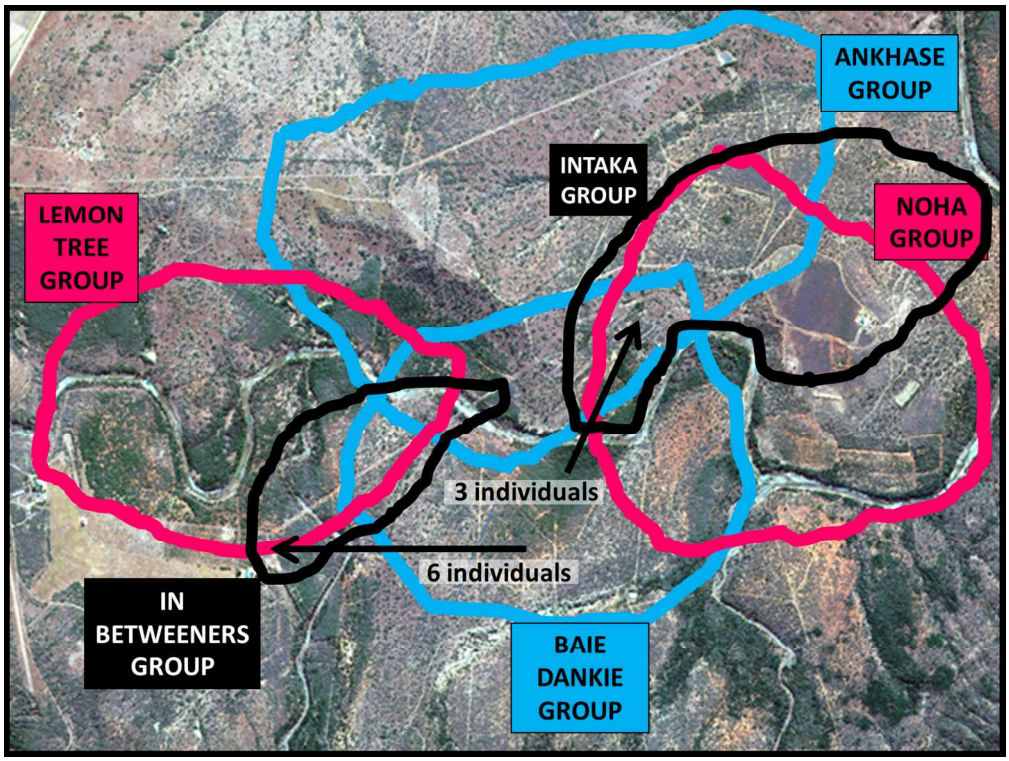

Figure 2: Map of the home ranges of two groups IB and IT that split from BD.

257x193mm (150 x 150 DPI)

Fig. 3

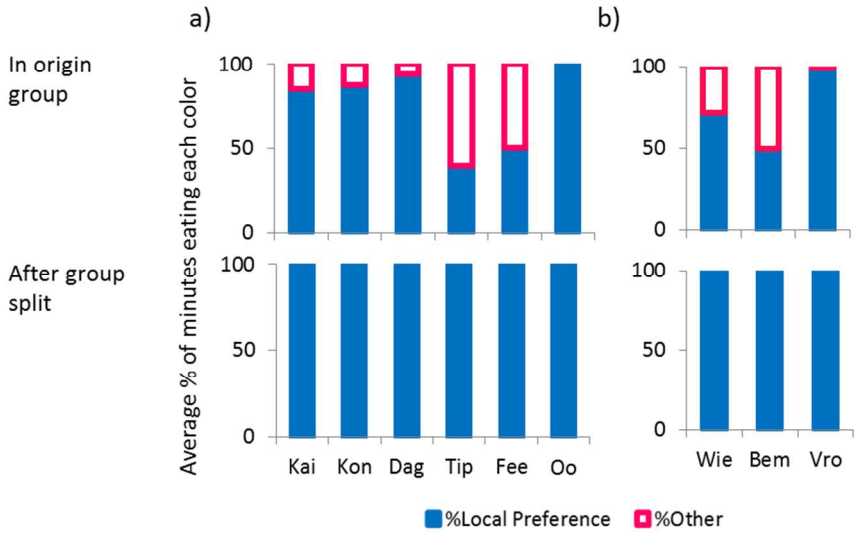

Figure 3: Average percentage of minutes spent eating the preferred color ('local preference') compared to the other color ('other') by individuals before (all recorded trials pre-fission where the individuals participated) and after split (1st trial) from the original BD group: a) for IB individuals; b) for IN individuals.

170x121mm (150 x 150 DPI)

Fig. 4

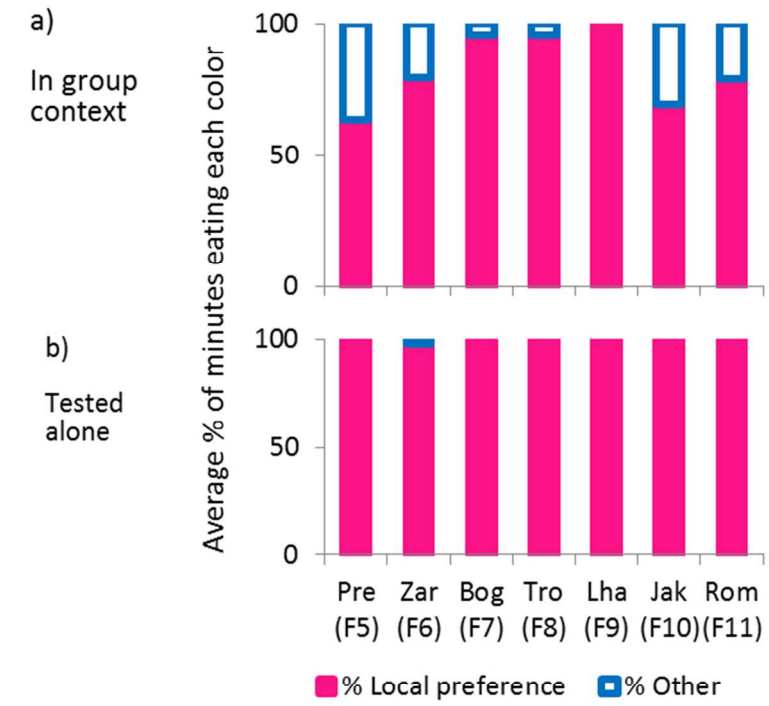

Figure 4: Average time (in minutes) spent eating the preferred color by low-ranking females of NH, in the group context and when tested alone.

133x125mm (150 x 150 DPI)

Fig. 5

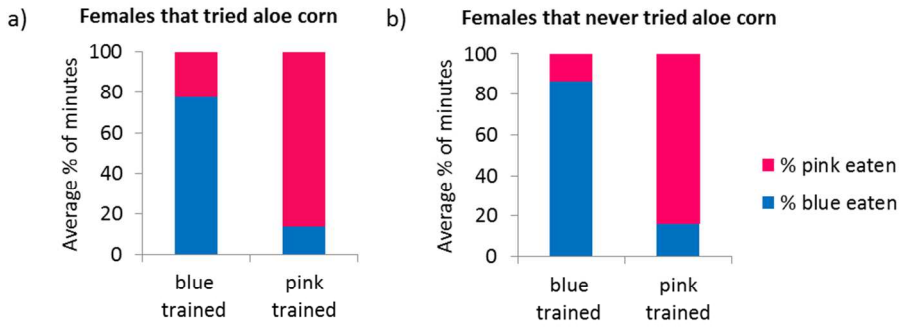

Figure 5: Average % of observed minutes eating corn of each color in both pink- and blue-trained groups: a) females that tried aloe corn during the training phase (n=20); b) females that never picked up a single corn piece treated with aloe (n=19).

190x93mm (150 x 150 DPI)

Fig. 6

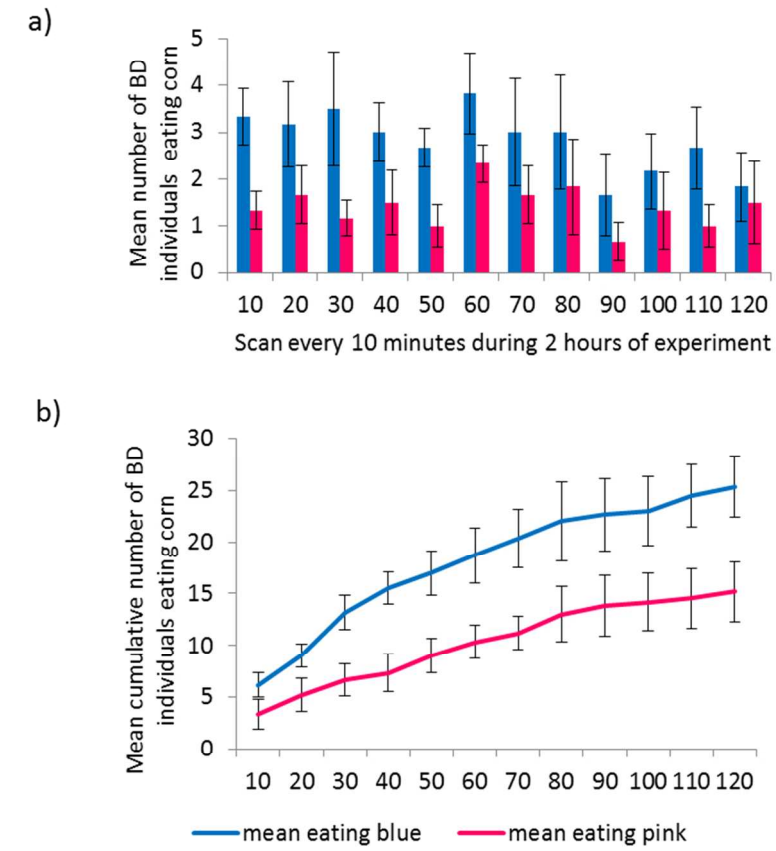

Figure 6: a) Mean number of BD monkeys eating the preferred color (blue) and the alternative color (pink) collected in 10-minute scans and expressed during the first two hours in experiments 1-6. b) Mean cumulative number of BD monkeys eating the preferred color (blue) and the alternative color (pink) across successive scan periods.

153x166mm (150 x 150 DPI)

Table 1.

Composition of the two splinter groups

	ID code	Age	Sex	rank in BD
IB	Kai	AD	F	9
	Dag	AD	F	10
	Tip	AD	F	11
	Fee	JU3	F	>11
	Kon	JU2	F	9
	Oo	AD	M	3
IN	Wie	AD	F	9
	Bem	AD	F	10
	Vro	AD	F	11

Table footnote:

Group composition of the two groups split from 'Baie Dankie' (BD) group; name codes (2 letter for males, 3 for females), age class (AD=adult, JU= juvenile with age in years), sex (F=female, M=male) and rank just before leaving BD (offspring have the rank of their mother). 'In-Betweeners' (IB) last experiment in BD group was 19th June 2012; the experiment after was 31st January 2013. 'Intaka' (IN) last experiment in BD group was 15th December 2012 and test after split was 15th March 2014.

Table 2.

Number of minutes splinter group females spent eating (a) pink or (b) blue in their origin group before they split off, during each of the six test sessions and in total.

a)

TEST	1	2	3	4	5	6	**total**
Kai	-	2	-	3	-	-	**5**
Dag	-	-	0	2	-	-	**2**
Tip	-	1	4	6	-	-	**11**
Wie	-	-	-	4	-	10	**14**
Bem	-	-	-	5	-	14	**19**
Vro	-	-	-	0	0	4	**4**

b)

TEST	1	2	3	4	5	6	**total**
Kai	-	4	-	15	-	-	**19**
Dag	-	-	2	7	-	-	**9**
Tip	-	5	1	1	-	-	**7**
Wie	-	-	-	9	-	4	**13**
Bem	-	-	-	2	-	2	**4**
Vro	-	-	-	22	12	28	**62**